

The Mechanism of Ciliary Movement.

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The mechanism of ciliary movement has been extensively studied from the morphological point of view, and although there is a general consensus of opinion as to the structure of the "ciliary apparatus," there is no adequate account of the functions of the various parts of the mechanism.

The material used for this work has been the gills of *Mytilus edulis*, and has already been described (Orton, 27). It is entirely due to the movement of the cilia that an efficient stream of water is kept passing on to the face of the gill, and that the food is moved up to the mouth of the animal. By means of carmine particles the existence of these currents is easily detected by the naked eye.

The production of a constant current of water in a definite direction implies that the cilia are capable of performing work in a remarkably efficient manner. If we watch the movement of a single cilium, it is obvious that the beat is divisible into two phases: (*a*) a very rapid forward or effective stroke; and (*b*) a slower backward or recovery stroke. It is during the rapid effective stroke that the cilium performs work on the surrounding medium, and in doing so, of course, expends energy. At the conclusion of the effective stroke these cilia possess no energy which can be used for work, but by the time the recovery stroke is completed a new supply of potential energy is available and is in turn converted into kinetic energy during the next effective stroke.

We are, no doubt, entitled to assume that the energy expended by a cilium has its origin in some chemical compound, either in the cilium itself or in the cell to which it is attached. Our main problem is to throw what light we can on the sequence of events which leads to the conversion of chemical energy into the kinetic energy of movement.

The first evidence which will be presented is that gained by an observation of the living cells under normal conditions.

I. THE STRUCTURE AND BEHAVIOUR OF NORMAL CILIA.

On the gill filaments are three main groups of ciliated cells—the lateral, the latero-frontal, and the frontal cilia (see Gray, 12). These cilia, like all other living cilia, appear to be optically homogeneous; they are strongly

refractive and possess a considerable degree of elasticity. In this respect Engelmann (8) expressed the view that: "Tous les organes vibratils sont résistants, très flexibles, et dans une large mesure parfaitement élastiques." The cilia of *Mytilus* are entirely independent of any control by the animal and are in constant motion during the life of the cells.

Lateral Cilia.

On the sides of each gill filament are three rows of rectangular cells, each bearing a brush of cilia. These are the lateral cilia (see figs. 1 and 2). The

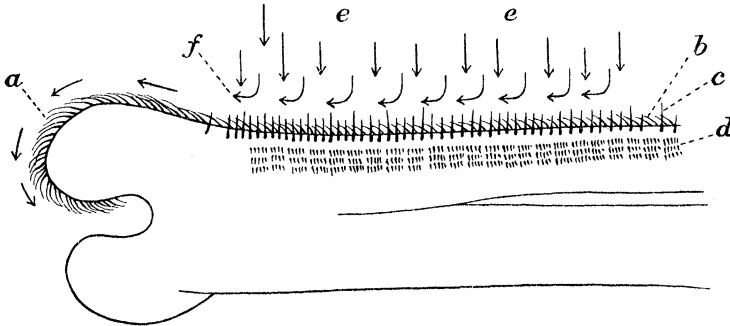


FIG. 1.—Lateral view of gill filament of *Mytilus* (modified from Orton). (a) Terminal cilia, (b) frontal cilia, (c) latero-frontal cilia, (d) lateral cilia, (e) vertical water current set up by lateral cilia, (f) direction of water current from frontal cilia.

effective stroke causes a strong current of water to flow on to the gill surface at right angles to it (see fig. 2). All the cilia arising from a single cell beat in the same phase, as do also the cilia of the three cells comprising each vertical row.

The most distinctive feature of the lateral cilia is their marked rhythm. The cilia on adjacent cells beat in succession, so that a continuous wave passes along the whole line of lateral cells from one end of the filament to the other; the wave passes in opposite directions on the two sides of the filament. This metachronial rhythm provides an interesting example of co-ordinated movement which is not associated with any visible nervous elements. Isolated individual cells from the lateral epithelium continue to exhibit active movement.

Latero-frontal Cilia.

It will be seen from fig. 2 that on reaching the surface of the gill the water columns set in motion by the lateral cilia meet the large *latero-frontal cilia*. During one phase of the beat these cilia rapidly pass from the form of straight rods to that of curved hooks, the point being directed towards the free surface of the filament. The cilia then flatten out more slowly; the

flattening begins at the base and proceeds to the point. These cilia also exhibit a certain degree of metachronism, but to a much less marked extent than

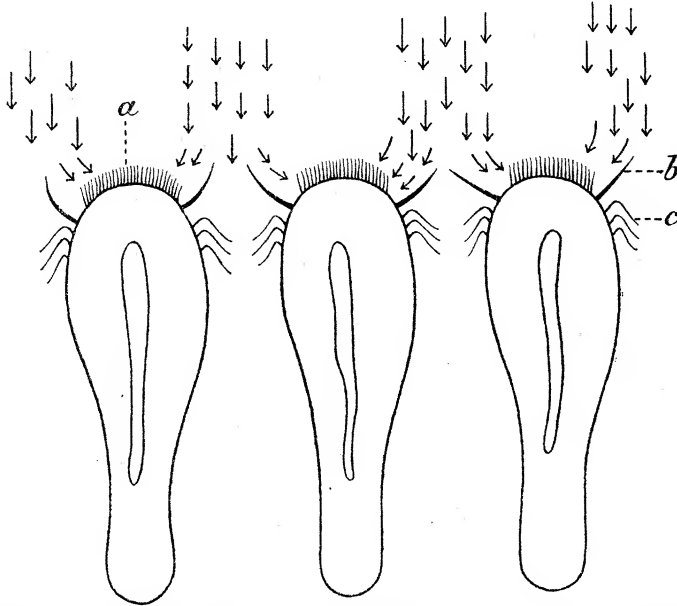


FIG. 2.—Transverse vertical section of three gill filaments, showing the deflection of the vertical current on to the frontal cilia. (a) Frontal cilia, (b) latero-frontal cilia, (c) lateral cilia.

the lateral cilia. The function of the latero-frontal cilia appears to be two-fold: (i) they act as vanes which deflect the water currents on to the surface of the filaments; (2) they keep the individual filaments apart, so as to give free play to the lateral cilia.

Frontal Cilia.

The whole of the flat frontal surface of the gill is covered by the frontal cilia, whose effective beat is parallel to this surface and directed towards its free edge (see fig. 1).*

When the movement is very greatly reduced in speed by the addition of gum arabic to sea-water, it is seen that, during the effective beat, the cilium behaves as a more or less rigid rod, which moves forward on a pivot at its base. During the recovery stroke, however, the cilium assumes entirely different properties—it is drawn back as a limp non-elastic body in which a stress is set up which starts at its base and is transmitted to the free end,

* At the end of the filaments the frontal cilia are modified so as to deflect the current towards the food grove and towards the oral end of the gill. These modified frontal cilia are very obvious, and will be referred to as the terminal cilia.

exactly as is the case in a fishing line during the backward movement of a cast. As the cilium moves back it loses its limpness, and at the end of the recovery stroke possesses a considerable degree of rigidity (fig. 3).

When movement is taking place fairly quickly the cilium does not appear

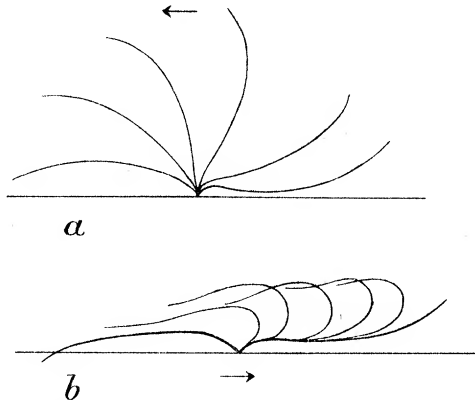


FIG. 3.—Diagram illustrating the form of the terminal cilia of *Mytilus* during (a) the effective and (b) recovery beats.

to straighten out completely at the end of the recovery stroke, but moves forward in the form of a sickle. During the final phase of the effective beat the hooked shape is always lost and re-develops during the recovery stroke.

It should be mentioned that the effective stroke is always quicker than the recovery stroke. When movement is very rapid it is impossible to see the cilium during the effective beat.

The change in the consistency of the cilium during the two phases of its beat appears to be an observation of considerable significance, but does not appear to have been commented on by other observers. The illustrations given in Verworn's (31) text-book of the cilia of *Urostyla grandis* appear to indicate the same phenomenon. The only detailed description of the movement of large cilia is that by Williams (32) of the cilia of a molluscan larva, which clearly indicates a difference in the elastic properties of the cilia during the two phases of the beat (fig. 4).

The effect of stimulation on a muscle fibre has been compared by Bayliss (1) to the conversion of a stretched lead spring to a stretched steel spring, so that the excited fibre is capable of expending energy in the form of work. The cilia of *Mytilus*, and to a still greater extent the cilia of Ctenophores, can be compared, with equal justice, to bent strips of lead and steel wire. *It seems fairly certain that the energy which is expended by the cilium is stored as tension energy.*

Let us now consider the point of origin of the stimulus to which the

movement of the cilium is the mechanical response. The cilia on adjacent cells of the lateral epithelium beat in a definite sequence. If, however,

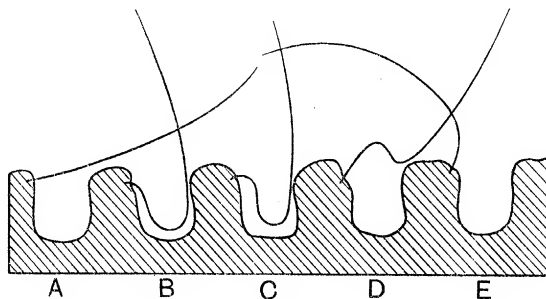


FIG. 4.—Diagram showing successive stages in the stroke of a cilium on the velum of a gastropod larva (after Williams). A, position of rest; B, position at end of recovery beat; C and D, stages during effective beat; E, end of effective beat.

individual cells are separated experimentally, they continue to exhibit active and prolonged movement (Gray, 12). All attempts to detect the operation of nervous elements in the epithelium, or in the cells themselves, have failed. It may be concluded, therefore, that these ciliated cells provide an example of an automatically contractile tissue. The cells are comparable to cardiac muscle cells; each cell is capable of independent movement, although, under normal circumstances, there is a definite co-ordination between adjacent cells.

When a piece of living *Mytilus* gill is teased in sea-water under the microscope, portions of the cuticular layer with attached cilia are often stripped away from the cells themselves. Such cilia are invariably motionless. It seems certain, then, that an *essential part of the mechanism lies in the cell itself*; as long as there is a small portion of normal protoplasm at

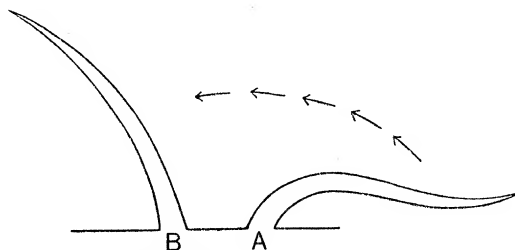


FIG. 5.—Diagram of cilia of *Pleurobrachia*. A is the position of rest; B is the end of the effective stroke, whose direction is shown by the arrows.

the distal end of the cell near the base of the cilium, the latter continues to move.*

* R. S. Lillie observed that detached but active cilia from the larva of *Polygordius* possessed a knob-like expansion at their proximal ends.

It is interesting to mention a few experiments which were performed on the ciliated plates of the Ctenophore *Pleurobrachia* (see fig. 5).

Like the lateral cilia of *Mytilus* there is here definite metachronal movement, but the movement of each cell is dependent upon a stimulus passing to it from the cell next to it. If the ciliated comb is cut, then all those cilia situated on the oral side of the cut cease to beat, and come to rest at the beginning of the effective beat. Any cell of this oral portion can be thrown into motion by stimulating the cell immediately above it. As far as one can see, these cilia resemble skeletal muscle rather than cardiac muscle, since some form of external stimulus is necessary to produce a mechanical response from the individual cells.

II. THE INFLUENCE OF THE ENVIRONMENT ON CILIARY ACTIVITY.

It has already been shown (Gray, 12) that a satisfactory medium for ciliary activity is provided by a Van't Hoff's solution containing NaCl, KCl, $MgCl_2$ and $CaCl_2$, in the same proportions as in sea-water, and whose hydrogen ion concentration is about $P_{H} 7.8$. We can therefore regard the other constituents of normal sea-water as unessential.

(a) *The Effect of Varying the Hydrogen-ion Concentration.*

The fact that the cilia on the gill of *Mytilus* cease to move when the hydrogen ion concentration of the surrounding medium reaches a limiting value, and that the cilia will resume their movements when the acidity of the medium is reduced (Gray, 12), led to the following investigation of Bernstein's well known hypothesis.

If the hypothesis be sound, then the inhibiting powers of an acid medium should be inversely proportional to the rate at which the acid can enter the cell. It has been shown that mineral acids enter living cells very slowly, if at all, whereas the fatty acids enter readily. Pieces of living gill, stained with neutral red, undergo no change in colour when placed in Van't Hoff solution, to which sufficient hydrochloric acid has been added to produce a hydrogen ion concentration of $P_{H} 3.4$: when placed in a similar solution, made acid with acetic or butyric acid, the gill instantly changes from a dull brick red colour to one of brilliant red—indicating that the acid has entered the cells. Corresponding facts apply to the alkalies: ammonia rapidly enters a living cell, whereas sodium hydroxide does not.

It is obvious, therefore, that a method is available for deciding whether the cessation of movement of cilia in an acid medium is due to an interference with the electrical properties of the cell surface, or whether the affected elements lie within the cell itself.

The procedure adopted was to determine the critical concentration of hydrogen ions in the external medium, which was just sufficient to cause complete stoppage of ciliary movement in 1 minute. A very large number of experiments were performed, whose results are summarised in the following Table :—

Acid.	Critical P_H concentration.	Acid.	Critical P_H concentration.
Hydrochloric	3·4	Oxalic	3·1
Sulphuric	3·1	Formic	4·0
Nitric	3·4	Acetic	4·8
Citric.....	3·4	Butyric.....	5·2

It will be observed that the mineral acids are of practically uniform efficiency, and the same hydrogen ion concentration of each is required to produce the same physiological effect. The fatty acids, on the other hand, form a series which is more efficient than the mineral acids, and the higher member of the series is distinctly more efficient than a lower member.

It has already been shown (Gray, 12) that, when ciliary activity has ceased in the presence of an acid, recovery takes place when the surrounding medium is made alkaline, so that it is possible to compare the effects of the weak and the strong alkalies as restoratives.

When movement has been stopped by means of a fatty acid, the cells rapidly recover in a solution which is not more alkaline than normal sea-water (P_H 7·8): by means of gill fragments stained with neutral red, this recovery can be seen to be due to the rapid rate at which the acid is removed from the cell. If, however, the cilia have been stopped by a mineral acid, recovery in normal sea-water is relatively slow (Gray, 12), so that such fragments form satisfactory material for testing the restorative powers of the various alkalies. In the following experiments, fragments of the same gill were exposed to a definite strength of mineral acid (HCl, P_H 3·3) for a definite period (5 minutes). Individual fragments were then transferred to normal sea-water, and to sea-water whose P_H had been raised to the same abnormally high value by NaOH and by NH_4OH respectively.

	Sea-water. P_H 7·8.	Sea-water. + NaOH. P_H 8·4.	Sea-water. + NH_4OH . P_H 8·4.
Movement began	12'	7'	1'
Full recovery	25'	19'	3'

The comparative efficiency of ammonia and sodium hydroxide is also seen from the following experiment. Fragments, after previous acid treatment, were transferred to sea-water whose alkalinity had been raised to a known value by NaOH and by NH_4OH .

P _H .	Time in minutes for full recovery in	
	NH_4OH .	NaOH.
9.5	$\frac{1}{2}$	5
9.2	$\frac{1}{2}$	7
9.0	$\frac{1}{2}$	8
8.7	1	8-10
8.5	3	10-12
8.4	5	12-15

The above figures all apply to fragments of the same gill after precisely the same acid treatment. The experiment was repeated several times with identical results.

It is therefore clear that *the weak acids which enter the cell are more efficient inhibitors of ciliary movement than are the strong acids which do not enter readily, and conversely the weak alkalies are much more efficient restoratives than the strong alkalies.*

It is impossible to accept the suggestion that the normal activity of the ciliated cells is upset by acids owing to a disturbance of the cell surface. The physiological effects of both acids and alkalies depend upon the ease with which these reagents penetrate to the cell interior. It may be noted that another series of experiments showed that the presence of neutral electrolytes in external medium has but little effect upon the efficiency of either acids or alkalies.

It is important to note that *the cilia come to rest in an acid solution by a gradual diminution in the rate of the whole beat, without any reduction in its amplitude.* Both the effective and the recovery strokes become slower, and there is often a marked pause at the beginning and end of each stroke, so that a complete beat may take as long as 10 seconds. It is difficult to imagine how this could occur where there is actual derangement of the contractile elements—since we would expect such to be attended by a gradual reduction in the amplitude of the beat.

Again, the cilia invariably come to rest at the end of the effective stroke; that is, in that position in which the cilium itself possesses no available potential energy.

Interesting evidence is available from a study of spermatozoa which are

known to possess a limited amount of reserve chemical energy. The effect of acid on such cells is precisely similar to that on ciliated cells (Gray, 13).

Cohn(5) has shown that when the movement of such spermatozoa has ceased in an acid medium, there is no loss of energy,* the conversion of chemical into potential energy has ceased, and can be switched on again by removing the acid from the external environment. *It seems highly probable, therefore, that the movement of cilia is stopped in an acid medium because there is no longer a conversion of chemical into potential energy.*

(b) *Metallic Ions.*

We have already seen that the cilia of *Mytilus* beat normally in an artificial solution containing NaCl, KCl, CaCl₂ and MgCl₂, and whose hydrogen ion concentration is the same as sea-water. On the whole, ciliary activity is remarkably independent on the absolute concentration of any particular ion or upon the exact ratio between different ions. In an investigation of the effects of individual ions it is necessary to maintain the normal hydrogen ion concentration and also the concentration of other ions in the solution. Further, in making a comparison between the effects of an ion on ciliary and on muscular activity, comparison must be made to a *spontaneously contractile* muscle (*e.g.*, the auricle of the heart). These facts explain the difference in the conclusions arrived at in this paper, and those of Lillie(20), Höber(16) and Mayer(23).

Experiments with Potassium Chloride.—If KCl be omitted from the external medium and its place taken by NaCl, the *lateral cilia* come to rest. The time taken for the movement to cease varies considerably in different gills. In most cases movement slows down after 5–10 minutes, and in less than 20 minutes the cilia are stationary. In a few cases in which the lateral cilia showed very active movement before the experiment, movement was continued in the absence of potassium for as long as 45–60 minutes; movement recommences vigorously on the subsequent addition of potassium, or on the addition of a small amount of alkali sufficient to raise the P_H to about 8.5. It should be mentioned that in several cases the lateral cilia ceased to beat in normal sea-water after about $1\frac{1}{2}$ hours, but on addition of a slight amount of KCl, vigorous movement took place. This may possibly be due to the fact that the blood of the animal contains a higher concentration of potassium than does normal sea-water, so that when isolated

* E. G. Martin(22) found that, in the presence of alkali, spontaneously beating strips of the ventricle of the tortoise gave out a constant total amount of energy for a unit mass of tissue.

in sea-water the gill is in an environment which may have a sub-normal concentration of potassium.

In contrast to the lateral cilia, the fronto-lateral, the frontal and the terminal cilia beat normally for very long periods (more than 48 hours) in a solution containing no potassium.

This contrast is paralleled by the action of such a solution when perfused through the heart of different molluscs. In the case of *Pecten* Mines(25) showed that potassium could be omitted from the perfusion fluid without any derangement of the heart beat; on the other hand, the heart of the *Octopus* gradually stops in such a solution (Kleefeld, 17), and can be revived on adding potassium.

If potassium is present in excess a similar contrast is found in its effects on the different cilia. Until the concentration of potassium is raised to about ten times the normal value, little or no effect is noticeable upon the cilia, although there is a tendency for a rapid secretion of mucus of the surface of the gill, which may clog the frontal and terminal cilia. Above this concentration the *fronto-lateral* cilia are affected in a curious way—they pass into a state of contraction which persists for a considerable period. At first the tips of the cilia remain bent at the end of the recovery phase of the beat, then a wave passes along a whole series of the cilia which accentuates this bend to a marked degree; this is followed by another wave in which one cilium after another remains fixed in a completely contracted position (*i.e.*, at the end of the effective beat). In this position the cilia often exhibit a curious quivering movement.

There is thus a regular “staircase” effect—similar to that found in the case of the heart.

If the concentration of potassium has not been too strong, the cilia recover on transference to normal sea-water after about 15 minutes. Even if contraction of the fronto-lateral cilia is brought about by a solution in which the whole of the NaCl in the Van't Hoff solution has been replaced by KCl, it is noticeable that after about 45 minutes, the cilia begin to recover in the original solution, the amplitude of the beat getting gradually larger until the complete beat is resumed. The rate of the recovery in such a solution, or in normal sea-water, is greatly hastened by the presence of alkali.

In all solutions containing excess of KCl, the beat and rhythm of the lateral cilia is well maintained and is often more rapid than in the normal gill; the frontal and terminal cilia are either unaffected or beat more rapidly than normal. Here again the differential action of potassium on different tissues is clearly illustrated.

Lillie and Höber have both emphasized the maintenance of ciliary movement

in the presence of excess of potassium, and have contrasted this with the depressant effect of such an excess on skeletal muscle. In view of the effect of KCl on the fronto-lateral cilia in preventing the recovery beat, it is interesting to note that this is also its effect upon skeletal muscle, viz., the latter is thrown into a state of prolonged contraction (Mines); the same thing occurs in the vertebrate heart (Burridge, 3).

The recent work of Kolm and Pick (18) on the effect of potassium on the heart brings out clearly three points: (i) the marked quickening effect on the automatically contractile auricles and sinus; (ii) the differential action on different tissues in the same organ, viz., auricles, ventricle; (iii) the prolonged contraction which is caused by high concentration of potassium: the contraction eventually passing off in the presence of the same perfusion fluid.

As far as I am aware there is no evidence against the view that in the case of automatically contractile tissues the effect of low concentrations of potassium salts is to increase the rate of movement, while stronger concentrations cause a prolonged contraction which is not, however, permanent.

The relative immunity of cilia as compared to a muscle cell to potassium is probably due to the fact that the latent period of the cilium is very much less than that of the average muscle cell, so that an environment which throws the latter into tonic contraction by increasing the rate of activity of the cell, has much less effect on the cilia.

The Effects of the Sodium Ion.—We have already mentioned that the absolute concentration of Na can be raised considerably without deranging ciliary movement. If the concentration of CaCl_2 , MgCl_2 , and KCl be kept constant, and the sodium chloride replaced wholly by isotonic saccharose, ciliary movement is well maintained for several hours.

It seems reasonable to conclude therefore that the sodium ion plays no specific rôle in activity—although it probably enters into the conditions of the general equilibrium within the cell.

The Effects of the Magnesium Ion.—If magnesium be omitted from the Van't Hoff solution, and its place taken by an appropriate amount of calcium, ciliary action is well maintained for many hours (more than 48 hours). Within wide limits a variation in the concentration of magnesium in the medium has little effect upon the form or rate of beat of the terminal cilia.

This fact is in accordance with observations upon the heart of the Octopus (Fredericq), the arms of Lepas (Mayer), and the heart of Salpa (Mayer)—all of which are insensitive to an absence of magnesium. The sensitivity of the heart of Pecten (Mines) is doubtless correlated with its high sensitivity to hydrogen ions (Mines).

In a subsequent paper, however, evidence will be presented which indicates that magnesium plays an important rôle in the economy of the cell.

The Effects of the Calcium Ion.—If calcium be omitted from the external medium, and the other conditions be the same as in normal Van't Hoff solution, prolonged ciliary movement takes place. The effect of the absence of calcium is, however, seen in the increased sensitivity of the cell to hydrogen ions. This is seen in the following experiment:—

P _H .	Duration of movement in	
	Van't Hoff solution, containing calcium.	Van't Hoff solution, without calcium.
7·8	More than 48 hours	More than 48 hours.
7·0	More than 48 hours	15-45 mins.

If, after the cessation of movement in the absence of calcium, the alkalinity of the solution be raised, rapid recovery takes place. If, on the other hand, calcium is added, the amount of recovery, at least for a time, depends upon the time which has elapsed between the cessation of movement, and the addition of the calcium. If the time is short, rapid and complete recovery takes place within 1 minute. If the time be prolonged, the recovery, on addition of calcium, is slow: the amplitude of the beat is regained almost at once, but the rate of both the effective and recovery strokes is slow, and there are often marked pauses at the beginning and end of each stroke. The whole phenomenon recalls the effect of acid, and one might conclude that the effect of the absence of calcium is possibly due to a change in the cell produced by a change in the hydrogen ion concentration.

The cessation of movement in the absence of calcium, and the recovery of movement on the addition of calcium or hydroxyl ions, is paralleled by the reaction of such solutions on the heart.

(c) The Effect of varying the Osmotic Pressure of the Surrounding Medium.

Although the cilia are not sensitive to slight changes in osmotic pressure, yet, if this exceeds a certain value, the cilia are rapidly brought to a complete standstill. On reducing the osmotic pressure, instant and complete recovery takes place. These facts are extremely easy to demonstrate, and can be repeated a great many times with the same piece of gill.

It does not matter whether the increase in osmotic pressure is brought about by the addition to sea-water of non-electrolytes or by balanced electrolytes (*e.g.*, 2½ M. Van't Hoff solution). In a solution which is not

quite strong enough to cause complete stoppage, it is noticeable that a reduced movement is maintained for a very long time (more than 24 hours); in such a solution the amplitude of the beat is much reduced, whereas the rate of beat is almost unaffected. In a solution which is strong enough to cause complete stoppage, the cilia remain in the position shown in the accompanying diagram (fig. 6), so that they are unusually conspicuous.

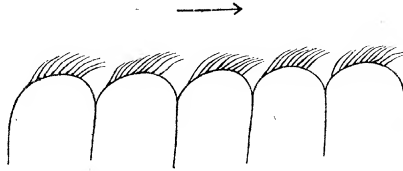


FIG. 6.—Diagram illustrating the appearance of the terminal cilia of *Mytilus* when brought to rest by high osmotic pressure of the external medium. The arrow shows the direction of the normal effective beat.

It is important to notice that the stoppage of the cilia in hypertonic solutions is brought about in an entirely different way to the stoppage in an acid solution, and it is therefore not surprising to find that the stoppage in hypertonic solutions is not influenced by the presence of hydroxyl ions, nor is the effect of an acid solution altered by reducing its osmotic pressure.

The effect of hypertonic solutions on muscular activity has not been extensively studied, but Demoor and Phillipson (7) have shown that the skeletal muscles of a frog lose their excitability to a direct stimulus when immersed in hypertonic Ringer solution; the muscles shorten somewhat, and the response is gradually abolished. These effects are entirely reversed by treatment with normal Ringer solution. Carlson (4) also found that the rate of beat of the auricles of the tortoise is unaffected by perfusion with hypertonic Ringer solution; the *amplitude* was, however, much reduced—and recovered in normal Ringer.

The fact that the amplitude of the beat is affected by an increase in the osmotic pressure of the external medium seems to indicate that a loss of water from the cell interferes not with the periodic liberation of energy, but with the actual contractile mechanism.

IV. SUMMARY AND DISCUSSION.

Let us now review the whole of the available facts, and attempt to form a working hypothesis of the nature of the ciliary mechanism. We have seen that the ciliated cells of *Mytilus* provide an example of an automatically contractile tissue; they differ from cardiac or smooth muscle in that their latent period is extremely short, and the rate of beat very much quicker than

corresponding muscle cell. The cilium is essentially an elastic fibre in communication with and dependent upon the protoplasm of the cell.* The cilium is capable of storing potential energy (supplied to it from the cell) in the form of tension, and of liberating this energy in the form of work. The amount of tension developed depends on the existence of free water in the cell. The rate at which the energy is stored and liberated by the cilium depends upon the hydrogen ion concentration of the cell interior. Whereas the rate of movement of the cilium depends almost completely upon the concentration of hydrogen ions inside the cell, it is largely independent of the presence of specific metallic ions (except in certain cases potassium) in the external medium.

A suggestion as to the way in which chemical activity within the cell may lead to the development of a tension in a fibrous structure (in the presence of water) is provided by the experiments of Fischer and Strietmann (9). These authors have shown that, if a piece of catgut, suspended in water, comes into contact with an acid, the fibre absorbs water and develops a considerable tension. The same phenomenon occurs in the presence of an alkali. In this experiment the essential conditions are: (i) the liberation of a chemical (acid or alkali) on the surface of a fibre; (ii) the presence of water. These facts form the basis of an hypothesis of muscular actions, but they can be applied with equal force to the ciliary mechanism. In the case of the muscle fibre, the production of an acid (lactic acid) during stimulation has been demonstrated. If the same fact be assumed to be true in the case of a cilium, then many of the facts stated in this paper receive a reasonable explanation. The rate at which lactic acid is produced from its carbohydrate precursor depends upon the hydrogen ion concentration of the medium (Kondo, 19). Hence, the rate at which chemical energy can be converted into potential energy will also depend upon the hydrogen ion concentration of the cell interior. It is therefore clear why the rate of the recovery stroke of the cilia of *Mytilus* is affected by acids which enter the cell. By our hypothesis, at the end of the recovery stroke the cilium possesses potential energy, owing to the stress set up in its elastic structure by the tension of those fibres at whose surface an acid is situated. This potential energy can only be liberated by the relaxation of the fibres; that is, by the removal of the acid. The rate at which the acid is removed will depend upon the degree of alkalinity of the surrounding cell contents. In other words, an explanation is available for the effect of acids and alkalies on the rate of the effective stroke of the cilium.

* The truth of this statement can be seen by reference to most text-books of histology, or to the work of Saguchi (29).

The alteration in the length or tension of a fibre exposed to acid depends upon the concentration of salts present (Fischer), or on the ease with which water can be drawn from the surrounding fluid. Hence, when ciliated cells are exposed to a solution whose osmotic pressure is capable of withdrawing a considerable amount of water from the cells, the amount of tension, set up by a normal amount of acid at the surface of the fibres, will be reduced; consequently, in solutions of high osmotic pressure, the amplitude of the beat is affected, and the cilia stop when the amount of free water is zero.

The above conception of the ciliary mechanism has two advantages: (i) it does not endow the cilium with any hypothetical structure; (ii) it brings the mechanism into line with what is known of other contractile tissues. There is, however, one corollary to the hypothesis which applies equally to cilia and to muscle cells. If the liberation of an acid at the surface of the ciliary fibrils enables the cilium to store potential energy and perform the recovery stroke—then, when ciliary activity ceases in the presence of an experimental acid, we must assume that the latter acid does not come into contact with the contractile fibrils, since the cilia come to rest with the fibrils relaxed. When, however, stronger concentrations of acid are used, the cilia stop partly (in some cases almost completely) contracted, and occupy a position near the end of the normal recovery stroke (see fig. 7). We may well

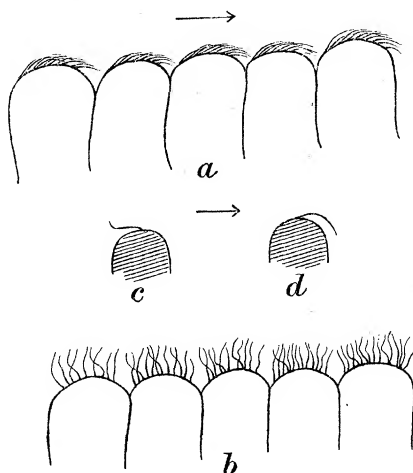


FIG. 7.—Diagram illustrating the effect of acid on the terminal cilia of *Mytilus*. (a) With acid just strong enough to stop cilia; note all the cilia stop at the end of the effective beat. (b) Acid of considerably greater strength; note the cilia come to rest between the two phases of the recovery stroke. (c) and (d) Positions at beginning and end of the normal effective stroke.

suppose that in this case the experimental acid has reached the contractile fibres. Precisely the same phenomena are found in the heart: weak

concentrations of acid stop the heart in diastole, stronger concentrations stop it in systole.

Finally, if the cilia of *Pleurobrachia* are considered, it will be obvious how very closely the known facts agree with the hypothesis of muscular action outlined by Hill and Hartree (15). The position of rest of these cilia is at the end of the recovery stroke, so that (like a striated muscle fibre) they possess a definite amount of potential energy, which can be released at the moment of stimulation. The cilium may be regarded as a series of fibres, B,* which are in communication with a network, A; the walls of the latter are kept stretched by the presence of water in the interstices of the network. It is this turgidity which provides the cell with the potential energy possessed at the position of rest. At the moment of stimulation, some chemical substance is set free at the surface of the fibres, B, which promptly take up water from the network, A, so that the cilium flies forward, owing to: (i) the liberation of the energy stored in the walls of A; and (ii) the tension developed in B. At the end of the effective stroke, the chemical substance is removed from the fibres, B, and the water flows away from the fibres (*e.g.*, by osmosis) into the interstices of the network, A, thereby stretching the cilium back to the resting position.

It should be understood that the above analysis of the ciliary mechanism is nothing more than a working hypothesis. At the same time the remarkable similarity between the conditions necessary for ciliary and muscular activity, coupled with the apparent similarity in the fibrous structure of the two types of cell, leads to the conclusion that the two mechanisms may be essentially similar. It is also clear that the same scheme might be applied to pseudopodial movement.

Summary of Experimental Results.

1. The cilium is capable of expending potential energy in the form of work as long as it is in organic connection with the cell protoplasm.
2. Each ciliated cell of *Mytilus* is capable of independent movement when isolated. The cilia of the Ctenophore *Pleurobrachia* require a definite stimulus to induce their beat. Both types of cilia show metachronal rhythm.
3. The cilium is an elastic fibre or bundle of fibres. In the large majority of cases the cilia are in communication with the cell protoplasm by means of intracellular fibrillæ.
4. The ciliary beat consists of a rapid effective stroke and a slower recovery stroke. The form of the recovery stroke often differs markedly from the effective stroke.

* The fibrous nature of these cilia is well seen in preserved specimens.

During the former the cilium resembles a slack string or fibre, whereas during the effective stroke its rigidity is distinctly greater.

5. When exposed to an acid solution of appropriate strength the cilia of *Mytilus* come to rest by a gradual slowing of the whole beat: the amplitude of the beat is not affected. The cilia always come to rest at the end of the effective stroke, *i.e.*, in the position in which the cilium possesses no convertible potential energy.

The cessation of movement in an acid solution is due to a change which takes place inside the cell, and not at its surface. Evidence is advanced which suggests that the presence of acid prevents the conversion of chemical energy into kinetic energy.

The effect of acid is entirely reversible by alkalies. The rate of the beat is most simply controlled by controlling the hydrogen ion concentration within the cell; up to a certain point the higher the internal alkalinity the more rapid is the ciliary beat.

6. Under normal circumstances the activity of the *lateral* cilia depends on the presence of potassium ions. This effect is probably due to the general effect of the ion in quickening the beat, which leads in the case of the *fronto-lateral* cilia to a state of prolonged contraction when potassium is in excess.

7. Ciliary activity is not sensitive to change in the concentration of magnesium or sodium in the external medium, although these ions play a part in the general equilibrium between the cell and its environment.

8. The absence of calcium ions may bring about a cessation of ciliary movement, which is antagonised by hydroxyl ions.

9. The reaction of cilia and of muscles to the various chemical constituents of their environment is essentially the same. The apparent differences are due to: (i) the greater sensitivity of most muscles as compared to cilia; (ii) the cilia have a much shorter latent period than most muscles; (iii) a ciliated cell cannot be regarded as directly comparable to a neuro-muscular system.

10. Cilia are brought to rest if the osmotic pressure of the external medium exceeds a certain value. The stoppage is brought about by a gradual reduction in the amplitude of the beat. These effects are entirely removed on reducing the osmotic pressure.

11. An hypothesis is put forward that the mechanism of ciliary movement is essentially the same as that of muscular movement.

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